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Ouwehand, Janne; Both, Christiaan

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African departure rather than migration speed determines variation in spring arrival in pied flycatchers

Janne Ouwehand* and Christiaan Both

Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, NL-9700 CC, Groningen, The Netherlands

Summary

1. Properly timed spring migration enhances reproduction and survival. Climate change requires organisms to respond to changes such as advanced spring phenology. Pied flycatchers *Ficedula hypoleuca* have become a model species to study such phenological adaptations of long-distance migratory songbirds to climate change, but data on individuals' time schedules outside the breeding season are still lacking.

2. Using light-level geolocators, we studied variation in migration schedules across the year in a pied flycatcher population in the Netherlands, which sheds light on the ability for individual adjustments in spring arrival timing to track environmental changes at their breeding grounds.

3. We show that variation in arrival dates to breeding sites in 2014 was caused by variation in departure date from sub-Saharan Africa and not by environmental conditions encountered en route. Spring migration duration was short for all individuals, on average 2 weeks. Males migrated ahead of females in spring, while migration schedules in autumn were flexibly adjusted according to breeding duties. Individuals were therefore not consistently early or late throughout the year.

4. In fast migrants like our Dutch pied flycatchers, advancement of arrival to climate change likely requires changes in spring departure dates. Adaptation for earlier arrival may be slowed down by harsh circumstances in winter, or years with high costs associated with early migration.

Key-words: annual cycle, bird migration strategy, impact assessment, passerine, protandry, wintering longitude

Introduction

Migration is an adaptive response to seasonally changing resources. Migrants profit from peaks in food abundance at their temperate breeding grounds, but avoid harsh conditions in winter (Alerstam, Hedenström & Åkesson 2003). Proper timing is considered a key element in the migratory lifestyle. An early arrival at breeding sites enhances an individual's chance to obtain a high-quality territory and mate (Lundberg & Alatalo 1992; Kokko 1999), which intensifies selection for timely and fast spring migration (Alerstam 2011; Nilsson, Klaassen & Alerstam 2013). Migrating too early can entail considerable costs of mortality when birds encounter adverse weather or poor

food supply upon arrival (Newton 2007). This intense selection on pre-breeding timing is expected to reduce variation in spring timing among birds, while post-breeding events are expected to be more variable (McNamara, Welham & Houston 1998). In addition to natural drivers of selection, human-induced changes in the environment do impose additional and increasingly important selection pressures. Afro-Palearctic migrants currently face rapid, ongoing environmental changes at their wintering grounds (Vickery, Ewing & Smith 2014) and also at their breeding grounds where the timing of peak food abundance advances as result of climate change (Both *et al.* 2009). It is yet unclear how well complex migratory life cycles are suited to adapt to such changing, and potentially less predictable, environments (Knudsen *et al.* 2011).

Pied flycatchers *Ficedula hypoleuca* have become a model species to study life cycle adaptation of long-distance

*Correspondence author. E-mail: janneouwehand@gmail.com

migrants to climate change, with an emphasis on how climate warming perturbs existing phenological adaptations at the breeding grounds (Møller, Fiedler & Berthold 2010). Long-term data from 25 European populations showed that flycatchers had the strongest advancements in laying dates in areas with most spring warming (Both *et al.* 2004). Observed responses have often been explained as phenotypic plasticity, with birds incorporating local environmental conditions into migration and breeding decisions upon approaching or after arrival at their breeding sites (Ahola *et al.* 2004; Both *et al.* 2004; Lehikoinen, Sparks & Zalakevicius 2004; Both, Bijlsma & Visser 2005; Hüppop & Winkel 2006; Both & te Marvelde 2007). Breeding ground studies also posed various claims about the underlying mechanisms and ability of migrants to alter their migration schedules to climate change without much data on individual time schedules (Knudsen *et al.* 2011), particularly outside the breeding season. A lack of change in spring arrival was interpreted as inflexibility associated with the mechanism controlling migration departure from the wintering grounds (Both & Visser 2001), while a later study suggested that temperature constraints during migration uncoupled spring departure from arrival at the breeding grounds (Both 2010).

Our limited knowledge on how flexible individual migration schedules are for free-living flycatchers comes from breeding ground arrival dates. Pied flycatchers in Spain and the Netherlands exhibit moderate repeatability in arrival dates, showing that timing is consistently different among individuals (Potti 1999 *females only*; Both, Bijlsma & Ouwehand 2016). This repeatability may hint at a heritability of innate, rigid difference in migration timing as found in laboratory studies (Gwinner 1996). Alternatively, consistency in timing can arise from reversible state effects that accumulate over an individual's life (Senner, Conklin & Piersma 2015). The latter has been described in American redstarts: early arrival at high-quality wintering sites advanced the timing of migratory departure in spring and subsequently led to earlier arrival timing and higher reproductive success (Marra, Hobson & Holmes 1998; Norris *et al.* 2004), which may subsequently carry over to earlier autumn migration.

Despite pied flycatchers being one of the best studied migrant species in relation to climate change, data on individuals' time schedules and decisions in the wild outside the breeding season are still lacking. Hence, it remains an open question as to what degree the observed variation and changes in arrival dates are driven by individual adjustments in migration duration or departure decisions (Tarka, Hansson & Hasselquist 2015), genetic adaptation (Jonzen *et al.* 2006) or ontogenetic changes (Both 2010; Gill *et al.* 2014) in time schedules. Here we make the crucial step by extending our understanding to phases prior to arrival at the breeding sites, because migrants' ability to adjust life cycles to environmental change will depend on the constraints and response modes

of all traits involved (Botero *et al.* 2015), including those during the migration phase.

In this paper, we aim to describe determinants of arrival date at the breeding grounds and their relation to preceding annual cycle events in the long-distance migratory pied flycatcher (hereafter, 'flycatcher') using light-level geolocators (hereafter, 'geolocators'). Tracking studies in several species showed that variation in timing of arrival within breeding populations is mainly determined by wintering departure (e.g. Tøttrup *et al.* 2012b; Callo, Morton & Stutchbury 2013; Jahn *et al.* 2013; Lemke *et al.* 2013). Strong correlations among timing events in spring may be expected if individual differences in migration schedules are rigid, and the pressure for early arrival at breeding sites is strong. If strong selection, however, reduced the variation in spring migration strategies among individuals, these correlations are likely weaker. Furthermore, studies looking at within-individual changes in other passerines showed that birds adjusted their spring departure (Studds & Marra 2011) or arrival timing (Baltontin *et al.* 2009) to external conditions in winter and during migration. Such fine-tuning to conditions along the migration routes, also proposed in pied flycatchers (e.g. Ahola *et al.* 2004; Both 2010), can thereby disrupt the predicted strong correlation among timing events in spring (Marra *et al.* 2005; Both 2010).

Migratory life cycles as we observe them will therefore not only depend on the underlying mechanisms, but also on an individuals' ability to behave accordingly. Individual differences in quality, condition and experience (Kokko 1999; McKinnon *et al.* 2014; Sergio *et al.* 2014) may further mediate migratory performance and pay-offs associated with specific migratory timing, meaning that individuals may adjust their migration decisions in response to intrinsic as well as external variables. Such 'mediated performance' was found for Spanish pied flycatchers where age and age-independent variation in wing length were correlated with male arrival dates (Potti 1998). In such circumstances, variation in spring migration schedules due to differences in endogenous programme or cue responses to photoperiod (e.g. Gwinner 1996; Maggini & Bairlein 2012) may not become visible in arrival dates: that is, the effect of variation in wing length and age on migration speed may override the underlying time schedules and hence determines individual variation in arrival timing (Potti 1998).

In this paper, we examine whether differences in timing between individuals persist or change over the course of a year by studying (i) correlations between sets of annual cycle events and, (ii) changes in population variability in timing over the course of the year. We specifically examine whether differences among birds in sex and breeding status, or breeding phenology contribute to the observed variation in migratory schedules. Because differences in wintering site location (here, longitude) have the potential to contribute to variation in timing, as recently shown between flycatcher populations (Ouwehand *et al.* 2016), we also test whether differences in wintering longitude

within our Dutch breeding population are correlated with timing of annual cycle events.

Tracking studies are a great tool to describe individual differences in avian migrants, but geolocator attachment may also mediate their performance (e.g. Costantini & Møller 2013) and thereby hamper reliable inferences about natural migration behaviour. We therefore first investigated geolocator and harness impact on survival and timing of arrival and egg laying.

With this study, we shed light on the role that individual adjustments during the migration period have in allowing long-distance migrants to successfully track environmental changes.

Materials and methods

STUDY SYSTEM AND FIELD OBSERVATIONS

Timing of migration in flycatchers was studied in 2013–2014 using field and geolocator data from a nest box population established in 2007 in the Dwingelderveld, The Netherlands (52°49' N, 6°22' E). The area consists of 12 plots located in forest patches dominated by oak, pine or mixed forest, with each 50 or 100 nest boxes (approx. 50 m apart). This population has roughly 300 breeding pairs, and an early breeding phenology compared to other European populations (Both & te Marvelde 2007). Between years, 5–20% of males that occupy a territory failed to attract a female (C. Both, unpublished data), hereafter referred to as 'unpaired males'.

Individuals were generally captured and ringed in the nest box halfway incubation (females) or when feeding 7-day-old chicks (males, females). Males still unmated in mid-May were caught during nest box advertisement or using mist nets. The age of unringed immigrants was estimated using feather characteristics, while age is known for locally hatched birds. Sex was determined from plumage characteristics and the presence of a brood patch. We visually monitored the spring arrival at least every other day from April until mid-May: based on territorial behaviour (males) or pair dates (females). Male and female identities as inferred from these observations were checked and confirmed when captured later in the season (for more details, see Both, Bijlsma & Ouweland 2016). Newly built nests were monitored at least every other day to determine the onset of egg laying. Actual hatching dates were defined by daily nest checks around predicted hatching dates.

GEOLOCATORS

In 2013, 100 adults were equipped with Intigeo-W50 geolocators without light stalk (Migrate Technology Ltd, Cambridge, UK). Breeding birds ($n = 28$ females, $n = 55$ males) were tagged prior to chick fledging (chick age: 6–15 day). We deployed the remaining geolocators on all available unpaired males still present at 20 May ($n = 17$). Most devices were attached using leg-loop harnesses, hereafter 'LL' (28 females, 52 males; following Rappole & Tipton 1991), but we also equipped 20 breeding males with full-body (FB) harnesses consisting of one loop around the neck and one around each wing, thus placing the device somewhat higher on the bird's back. A possible advantage of a FB harness could therefore be that it places the tracking device closer to the gravity

centre of the flying bird. We performed this pilot study with FB harnesses to test whether they reduce the impact of geolocators on birds' behaviour and performance. A FB harness may potentially increase drag (Bowlin *et al.* 2010), but field studies using them have not found negative effects (e.g. Åkesson *et al.* 2012). Body mass at the time of logger deployment was between 11.2 and 13.7 g (mean = 12.3 g, $n = 98$); geolocators weighed *c.* 0.52 g including harness (range = 0.50–0.55 g; $n = 24$), which corresponded to 4.2% of the bird's body mass on average (range = 3.9–4.6%; $n = 24$).

We retrieved geolocators by capturing individuals at their nest box or using mist nests in 2014 ($n = 26$) and 2015 ($n = 3$). Geolocation data were downloaded and, if still recording data upon recapture, linearly corrected for clock drift (max = 85 s). We determined twilight times with TransEdit (British Antarctic Survey, Cambridge, UK) on transformed light data [i.e. $\log(\text{Lux}) \times 20$] with thresholds between 6–12, and a minimum dark period of 4 h (data at dryad: doi: 10.5061/dryad.k6q68). We used a loess function in the R-package GEOLIGHT 1.03 (Lisovski & Hahn 2012) to remove clear outliers from the transition file. We used geolocator-specific k -values to define when points are outliers (range: 2–3), because data quality varied among loggers. Per geolocator, we tried various k -values and chose the value that excluded most late sunrises and early sunsets (i.e. points influenced by shading), without filtering out many early sunrises and late sunsets.

Timing and duration of migration

Filtered transition files were used to define timing of major migratory events: that is, onset of autumn migration, arrival at the stationary non-breeding area, onset of spring migration and arrival at the breeding grounds. Migration schedules were not inferred at a finer scale to prevent that differences in the number of 'stopovers' are just due to data quality (within and between birds) rather than movement behaviour. The breeding period in Europe and non-breeding residency period in sub-Saharan Africa (hereafter, 'wintering') could also include smaller-scale (especially latitudinal) movements, but not large-scale directional movements such as during autumn and spring migration (Fig. S4, Supporting Information). To extract timing events, we used the ChangeLight function in the R-package GEOLIGHT (Lisovski & Hahn 2012), which marks transitions between stationary and movement periods based on the quantile probability threshold ' Q ' and a minimum stopover of 3 days. We used geolocator-specific Q -values (ranged: 0.88–0.95) because the interpretation of Q is influenced by data quality. We chose Q -values that picked up more changes than we needed (between 10 and 18 periods) to increase our ability to extract movements during periods when shading events were dominant. In several cases, single outliers were thereby regularly erroneously defined as movements. Therefore, short periods as defined by ChangeLight were manually pooled into four major phases, based on position overlap of periods (plotted with preliminary sun elevation angles obtained by Hill-Ekstrom calibration) and directional changes in twilight times, longitude and latitude (Fig. S4). Gradual movements can be difficult to detect with the ChangeLight function during periods when data quality is low (Ouweland *et al.* 2016), possibly because day-to-day shading exceeds the distance of daily movements. We therefore compared the migration schedule inferred from ChangeLight with visual inspections from longitudes over time. Three of 26 spring events, either in winter departure or breeding arrival, were not

recognized: with differences of more than 2 weeks from the closest event inferred via ChangeLight. In autumn, deviations in breeding departure or wintering arrival were more common: that is, 5 days or more for 13 of 54 events (of which $n = 3$; range 10–15 day). In such cases, the particular movement event (i.e. the one not recognized by ChangeLight) was adjusted based on visual inspection of directional changes in twilight times and longitude. Our method is thus not fully standardized, but strong resemblance between geolocation and field estimates of spring arrival suggests a high accuracy of our approach to define timing events, at least in spring (Both, Bijlsma & Ouweland 2016). Although autumn schedules may seem less accurate (by gradual movements, stronger shading), the clearer longitudinal component in autumn migration compared to spring helps to reliably infer autumn migration events (Fig. S4; Ouweland *et al.* 2016).

Two other migratory events could be inferred with high exactness from our raw light data files: twice a year a short period occurred with smooth transitions without shading events and high maximum daily light values. Such events lasted 1–2 day light curves and suddenly ended with an abrupt occurrence of shading during the day. Such bright periods refer to short windows of diurnal flight (hereafter, 'diurnal flight') that likely enable individuals to rapidly fly non-stop to cross barriers (Ouweland & Both 2016a). These diurnal flight periods are associated with large changes in twilight times and major migratory movements and initiated from major fuelling sites: that is, the Iberian peninsula in autumn and the wintering locations in spring (Ouweland & Both 2016a). Autumn diurnal flight was detected in all birds and spring diurnal flight in 14 of 15 birds where devices worked long enough to record the onset of spring migration.

Wintering longitude

GeoLight was used to calculate longitude positions (but not latitude) twice each day. Since flycatchers show site fidelity to wintering sites (Salewski, Bairlein & Leisler 2000), we used the median longitude in January to approximate wintering locations. Using such a core dry season period reduces effects of shading and hence improves longitude precision (Ouweland *et al.* 2016). Precision (i.e. 25–75% quartile range) was on average, 0.50°W and 0.45°E of the median longitude.

As shading conditions can change sharply in flycatchers even within stationary periods (Ouweland *et al.* 2016), obtaining reliable geolocation estimates of latitude is difficult. Changing shading conditions limits the use of in-(breeding)habitat calibration to obtain appropriate sun elevation angles for the whole year and challenge the assumption of stable shading to perform Hill–Ekstrom calibration (see Ouweland *et al.* 2016). Moreover, precision of latitude will easily cover the whole latitude range in winter and is therefore not used for our within-population comparison of events.

STATISTICAL ANALYSES

Geolocator impact

We explored potential impact of geolocation deployment and harness type by comparing local return rates, and spring arrival and laying dates of birds with and without geolocators (hereafter 'controls') for 2013–2014 (data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k6q68>). Controls

consisted of birds that raised chicks in the same study plots as the geolocator individuals (except for four individuals in one plot, with less systematic catching and monitoring). Proper controls for unpaired males were missing, as all unpaired males were equipped with geolocators. We excluded one female returning without geolocator from the impact analysis. Local annual return rates were the number recaptured in 2014 divided by the number within a group in 2013.

To test whether geolocators affected return rates of flycatchers, we used generalized linear mixed models (GLMMs) with binomial errors and logit link function in the R-package 'lme4' (Bates & Maechler 2009). We first test whether harness type ('LL', 'FB', 'controls') affected return rates within breeding males. Because differences among harness types were found, we did not pool geolocator birds equipped with different harness types in further analyses. We tested whether geolocators affect return rates of breeding birds using a GLMM with 'device' (geolocator with LL, control) and 'sex', and its two-way interaction.

Moreover, we tested whether geolocators impacted spring arrival and female egg laying in 2014. We only included arrival estimates until 20 May, as arrival observations after this period were less systematic and likely refer to individuals that first tried to settle in other areas. We also excluded two egg laying dates that probably refer to replacement clutches: that is, being 20 day later than the population mean date. We aimed at comparing arrival and laying dates between years within individuals as both traits were found repeatable (Both, Bijlsma & Ouweland 2016). To account for year and sex differences in timing, we defined timing as the 'relative' difference in days from the year- and sex-specific mean for the population (from Both, Bijlsma & Ouweland 2016). Using linear models (LMs), we added relative timing in 2013 as covariate when testing for geolocator impact on timing only if it significantly explained relative timing in 2014. This was true for male arrival and when arrival timing of sexes was pooled, while 'relative timing 2013' dropped from the model when testing females separately.

Timing of annual cycle events

We first analysed how timing between consecutive migratory events were correlated using LM (i.e. from breeding departure until spring arrival). Because we aimed to understand which event was most important to explain variation in arrival dates, we tested the strength of correlations between timing of spring arrival and any of the preceding timing stages. If no geolocation estimate was available for spring arrival timing (i.e. $n = 15$ geolocators stopped working before birds arrived at their breeding grounds), we used field estimates of arrival instead, as these two measures are highly correlated (i.e. $r = 0.98$, $n = 13$; Both, Bijlsma & Ouweland 2016).

We hypothesized that variation in migration timing decreases chronological towards the breeding season and tested this by examining the rank order of temporal variation (i.e. standard deviation of a stage) across migration stages. We excluded 'spring diurnal flight' as it appears to define the same event as spring departure time (see Results), which agrees with strong resemblance in longitudes from where birds initiated these events (Ouweland & Both 2016a). The onset of diurnal flight (inferred from raw data) thereby confirms the accuracy of our approach, at least to infer spring departure. We used all 14 individuals with complete data for the five remaining stages. As we had the

hypothesis of reduced variation towards the breeding season, we used one-tailed Spearman rank correlations in the R-package 'PVRANK' (Amerise, Marozzi & Tarsitano 2015) to test whether observed ranks followed the expected negative rank correlation, using conservative *P*-values. We expected variation in timing partly to arise from sex differences and thus repeated the above analyses with an individual's timing expressed relative to its sex-specific mean for each event, in case we detected a trend or significant sex differences in timing (see Table S2).

Next, we explored how migration timing during the annual cycle changed depending on its sex and breeding state. We built a linear mixed-effect model of relative timing across five migration stages with individual as random effect, using the 14 individuals with complete data. We examined whether birds in different sex/breeding categories (i.e. 'unpaired male', 'breeding female' or 'breeding male') showed different changes in relative timing (dependent): that is, the difference of an individual to the mean date (1 = 1 April 2013) per stage for the entire population. We examined the main effect of 'sex/breeding category' and the 'sex/breeding category' \times 'stage mean date' interaction and evaluated their significance using likelihood ratio tests against reduced models (with maximum likelihood). This interaction allowed us to test whether time schedules of birds from the different breeding categories progress in different ways, that is become earlier or later over the year relative to the overall mean date. Parameter estimates were obtained from minimal adequate models with restricted maximum likelihood. If differences among sex/breeding categories were found, we *post hoc* determined how big these differences were within each stage using LMs.

For breeding birds, we tested whether hatching date of their clutch affected the timing of subsequent migration events using LMs. However, returning geolocator females hatched their broods in 2013 earlier than geolocator males (Table S4), possibly as a result of non-random return of, mainly early, geolocator females (Fig. S2). To prevent merely reporting sex differences, rather than the influence of egg hatching date *per se* on timing, we expressed hatch dates and the (dependent) timing events as days relative to the sex-specific mean date, if sex differences occurred (Table S2).

Finally, we used LMs to determine whether wintering longitude affected spring departure and arrival, or was affected by hatch date, autumn departure and wintering arrival.

All analyses were performed in R 3.2.2 (R Development Core Team 2015). Timing values are expressed as means \pm SD unless reported otherwise.

Results

GEOLOCATOR IMPACT

In 2014, 27 of the 100 adults returned that were equipped with geolocators in 2013 (one lost its device). Three more birds returned in 2015. Return rates are based on birds returning in 2014 (Table S1) and are thus minimal estimates of local survival rates.

Males deployed with a FB harness returned significantly less than males with LL harness and controls ($\chi^2 = 8.9$, d.f. = 2, $P = 0.012$; 10% vs. 34% and 43%, respectively). We could not detect significant differences between harness types on the relative spring arrival of

breeding males in 2014 ($F_{2,36} = 1.2$, $P = 0.30$: accounting for arrival date 2013). However, FB males arrived 6–8 day later than controls, while for LL males this difference was negligible (+0.05 day; Fig. S1a). Because FB males had significantly reduced return rates and arrived almost 7 days later, the subsequent analyses and results exclude the two FB males.

We found no significant difference in return rates of breeding geolocator adults (males + females) with LL harness (30%) compared to the 35% observed in control birds ($\chi^2 = 1.3$, d.f. = 1, $P = 0.26$). Females had a lower local return rate ($\chi^2 = 5.0$, d.f. = 1, $P = 0.025$; 27% vs. 40% for males), but including sex did not show an effect of carrying a geolocator ('device + sex': $\chi^2 = 1.9$, d.f. = 1, $P = 0.16$) nor did the interaction ('device \times sex': $\chi^2 = 0.1$, d.f. = 1, $P = 0.75$). Return rates of unpaired LL males were not significantly different from breeding LL males ($\chi^2 = 0.2$, d.f. = 1, $P = 0.63$; 41% vs. 34% returned, respectively).

The timing of relative spring arrival in 2014 for LL geolocator birds that bred in 2013 was, on average, 2.8 day later, which was not significantly different from control birds ($F_{1,64} = 2.0$, $P = 0.16$: accounting for arrival date in 2013). This delay was mainly caused by non-significant differences in females: geolocator females were 3.2 day later in spring arrival ($P = 0.37$) and egg laying date ($P = 0.26$) in 2014 when compared to controls (Fig. S1a,b).

We found no evidence that early and late birds responded differently to device deployment ('relative date 2013 \times device': $F_{1,64} = 0.01$, $P = 0.98$).

TIMING OF ANNUAL CYCLE STAGES

Arrival date at the breeding grounds was positively correlated with departure from the wintering grounds (Fig. 1a). The steep slope and tight correlation demonstrate that spring migration duration was similar across individuals (mean = 13.6 ± 2.9 day; range = 9–18 day; $n = 14$), whereas individuals varied in departure date by up to 5 weeks (Table S3). Departure from the wintering grounds was quickly followed by the onset of 'diurnal flight' (Fig. S3b), which suggest that most birds almost immediately started with prolonged flights to cross the Sahara desert.

Post-breeding stages were positively correlated (Fig. 1c–e): later departing individuals from the breeding grounds showed later onset of diurnal flight in fall and subsequently arrived later at their wintering grounds. We found a tendency for individuals with later hatching offspring to have a later diurnal flight onset in autumn ($P = 0.084$), but none of the other subsequent stages were correlated with hatching date (Table S4). Yet, birds that departed late from the breeding grounds advanced their time schedules somewhat over the course of autumn migration (Fig. 1c). Migration in autumn took with 34.3 ± 7.1 days

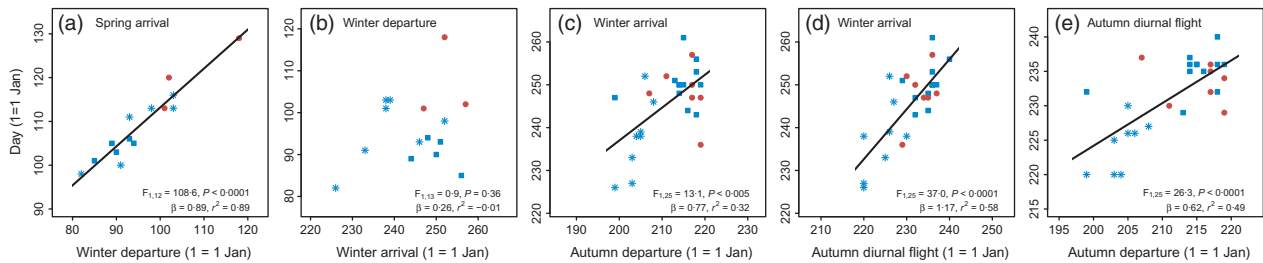


Fig. 1. Correlations between timing of consecutive migration events of pied flycatchers over 2013–2014 (breeding males in squares, unpaired males in stars, females in dots), as inferred from geolocation and/or field data. Solid lines show significant relations ($P < 0.05$).

(range = 17–48 day; $n = 27$) more than twice as long and was more variable than in spring, as indicated by less tight correlations in autumn (Fig. 1a,c).

We found no correlation between winter arrival and spring departure (Fig. 1b), nor between breeding arrival and autumn migratory events such as wintering arrival ($F_{1,21} = 2.2$, $P = 0.15$), autumn diurnal flight ($F_{1,21} = 0.1$, $P = 0.76$) or autumn departure ($F_{1,21} = 0.2$, $P = 0.67$). Variation in autumn timing thus disappeared during the half year they stayed in sub-Saharan Africa (216 ± 11 day, range = 194–231 day). Despite this buffering in winter, variation in spring departure was large, up to 5 weeks. The temporal variation in a stage did not diminish as birds approached the breeding grounds (Spearman rank test on SD: $r_s = 0.60$, $n = 5$ stages, $P = 0.78$, $n = 14$ birds). This was partly caused by sex differences in spring departure and arrival, with males migrating 2 weeks earlier than females (see Table S2). However, even if we expressed timing relative to the sex-specific mean in each stage, temporal variation did not decrease when approaching the breeding grounds (Spearman rank test on SD: $r_s = 0.50$, $n = 5$, $P = 0.74$): the range in spring departure dates was still 3 weeks.

Breeding status and sex influenced how an individual's relative timing changed over the season (Fig. 2), as shown by the interaction of 'sex/breeding category \times stage mean date' in the set of individuals for which we had timing across all migration stages (LMM: $\chi^2 = 14.1$, d.f. = 2, $P < 0.001$, marginal $R^2 = 0.51$). A *post hoc* analysis revealed that breeding males were about 10 days later than unpaired males in departure from the breeding grounds ($F_{1,9} = 44.1$, $P < 0.0001$, $R^2 = 0.81$), autumn diurnal flight ($F_{1,9} = 18.9$, $P < 0.005$, $R^2 = 0.64$) and arrival at the wintering site ($F_{1,9} = 5.7$, $P < 0.05$, $R^2 = 0.32$). In spring, these breeding males left 5 days ahead of unpaired males (a non-significant difference, $P = 0.25$) and arrived 4–5 days earlier at the breeding sites ($P = 0.23$). Males with breeding duties showed similar departure, diurnal flight and arrival at wintering sites in autumn as females (all $P > 0.50$) but were almost 17 days ahead of females in spring departure and arrival (respectively: $F_{1,6} = 13.6$, $P < 0.011$, $R^2 = 0.64$; $F_{1,6} = 21.6$, $P < 0.005$, $R^2 = 0.75$; Fig. 2). Spring migration duration was similar for breeding males, females and unpaired males ($F_{2,11} = 0.11$, $P = 0.90$).

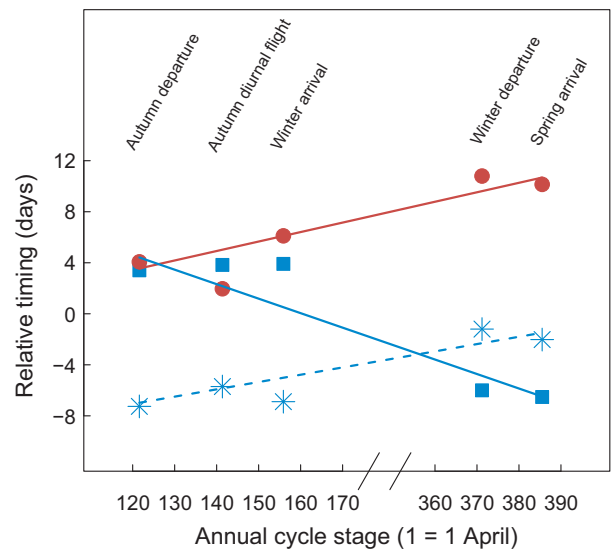


Fig. 2. Changes in timing across the annual cycle for breeding females (dots, solid line; $n = 3$), breeding males (squares, solid line, $n = 5$) and unpaired males (stars, dotted line, $n = 6$). Relative timing is the mean group difference from the stage mean date in all 14 individuals. The x-axis shows the stage mean date. Lines are inferred from linear mixed models.

Male breeding status did not influence at which longitude an individual spent the winter ($F_{1,18} = 1.5$, $P = 0.24$), nor were there differences among the sexes ($F_{1,25} = 0.2$, $P = 0.66$). Wintering longitudes ranged from 10–15°W to 5–17°W (mean = $7.4^\circ \pm 1.0^\circ$ W). Within this range, there were no correlations between wintering longitude and wintering site arrival ($F_{1,25} = 0.1$, $P = 0.74$) nor the onset of autumn migration ($F_{1,25} = 0.05$, $P = 0.88$). Wintering longitude also did not affect winter departure ($F_{1,13} = 0.2$, $P = 0.69$) or spring arrival dates ($F_{1,21} = 0.3$, $P = 0.57$) neither when considering sex differences in spring timing (see Tables S2 and S4).

Discussion

This paper aims to understand individual variation in timing of the annual cycle in a long-distance migrant, to elucidate the potential to advance spring arrival and breeding dates in response to climate change. We found that during spring migration, pied flycatcher males and

females travel in only 2 weeks from West Africa to their Dutch breeding sites. Most birds almost immediately started these migrations with a prolonged flight to cross the Sahara desert. Individuals varied in departure dates, but not migration duration, resulting in a strong positive correlation between wintering ground departure and spring arrival. These patterns were unlikely affected by artefacts of geolocator deployment, as we found no differences between geolocator birds equipped by LL harnesses with a large control group. Thus, in our study, variation in spring arrival dates was caused by variation in departure dates and not by variation in migration rates.

Annual variation in mean population arrival dates of flycatchers has been interpreted as variation in migration speed in response to conditions en route, because of correlations with weather patterns encountered (e.g. Lundberg & Alatalo 1992; Ahola *et al.* 2004; Both, Bijlsma & Visser 2005; Hüppop & Winkel 2006). Paradoxically, our data on individuals suggest little potential for Dutch flycatchers to migrate faster, as they covered >5000 km during spring migration in <2 weeks, leading to an estimated migration rate of *c.* 370 km day⁻¹ (i.e. minimal great-cycle distance/migration duration), which is considerably faster than similarly sized passerines (e.g. Kristensen, Tøttrup & Thorup 2013; Lemke *et al.* 2013; McKinnon, Fraser & Stutchbury 2013; Hahn *et al.* 2014; McKinnon *et al.* 2014).

Spring departure dates varied over 3 weeks in males and hence there seems large potential for selection to advance arrival dates via changes in spring departure schedules. The population variation in spring departure and arrival was also not reduced relative to other migration stages, despite the assumed fitness benefits of properly timed arrival at the breeding sites. As in several other long-distance migrants (Newton 2008), flycatchers arrived over a considerable period each spring (Lundberg & Alatalo 1992; Both, Bijlsma & Ouwehand 2016). Our data support the notion that variation in arrival date is caused by individuals varying in departure date from their wintering grounds. Similarly, strong positive correlations between winter departure and spring arrival dates were found in great reed warblers *Acrocephalus arundinaceus* (Lemke *et al.* 2013), red-eyed vireos *Vireo olivaceus* (Callo, Morton & Stutchbury 2013) and Western kingbirds *Tyrannus verticalis* (Jahn *et al.* 2013). In our study, part of the variation in departure schedules was explained by males departing before females. This fits with males arriving prior to females in our population (Both, Bijlsma & Ouwehand 2016), but the extent of protandry can vary among populations (Schmaljohann *et al.* 2016). Even when taking into account the observed protandry, large variation in spring departure schedules still occurred.

Variation in wintering ground departure was unrelated to timing events in autumn, and thus we did not find maintenance in timing differences across the annual cycle. Instead, the differences in time schedules as found in autumn shifted relative to timing differences in spring

(e.g. in diurnal flight events). The rank order in timing among birds broke up during winter, also when sex differences in spring timing were accounted for. Such shifts in time schedules were also found among different barn swallow *Hirundo rustica* breeding populations (Liechti *et al.* 2014). We expected consistency if endogenous schedules determine autumn and spring migration, or if individuals with an early autumn migration and arrival at their wintering sites have an advantage later in the annual cycle – for example via prior occupancy of good wintering sites – that enables them an earlier departure and arrival in the following spring. We did not detect correlations that hint at the latter: for example, wintering longitude was not correlated with an individual's arrival at or departure date from the wintering grounds. Previous studies that found similar patterns have often suggested that autumn migration timing is more easily adjusted, while spring migration is under stronger selection and/or less flexible (Stanley *et al.* 2012; Senner *et al.* 2014; Sergio *et al.* 2014).

How annual cycles developed across the year depended strongly on whether or not birds bred. Unpaired males left their territories about 10 days ahead of breeding males. Despite their earlier winter arrival, most unpaired males started spring migration later than breeding males and hence arrived later at the breeding sites. Intriguingly, the probability that a returning geolocator male got mated in 2014 did not depend on their spring arrival timing *per se*, but rather on their prior breeding status. Only 17% of the males that were unpaired in 2013 were found breeding in 2014, while 67% of males that bred in 2013 also bred in 2014. This hints at intrinsic quality differences in birds that affect both breeding prospects and migration schedules. Intrinsic differences in spring departure may be dictated by genetic and photoperiod-induced migratory schedules (Maggini & Bairlein 2012; Bazzi *et al.* 2015; Saino *et al.* 2015), although other factors such as wintering conditions or age can also influence departure decisions (Kristensen, Tøttrup & Thorup 2013; McKinnon *et al.* 2014; Sergio *et al.* 2014; Cooper, Sherry & Marra 2015; Mitchell *et al.* 2015). In our study, male breeding status was also associated with age: five out of six non-breeders deployed with geolocators were in their second calendar year, whereas only two out of ten breeders were second calendar year males. Annual cycle schedules are expected to vary with age: arrival date advances with age up to 4 years in male flycatchers (Potti 1998; Both, Bijlsma & Ouwehand 2016). Differences in breeding prospects and migration schedules between breeders and non-breeders may thus be an age effect. Such age effects on arrival timing have also been shown in recent tracking studies, although these are – contrary to our findings – often reflected in their migration speeds (as, e.g., in McKinnon *et al.* 2014; Sergio *et al.* 2014; Mitchell *et al.* 2015; Schmaljohann *et al.* 2016).

Whether the variation in spring departure date is flexible or mostly reflecting innate individual trait differences

is unknown, but it shows the potential for adjustment of arrival date through changes in departure. This fits with the 10-day advance in spring recovery dates of pied flycatchers in North Africa across 1980–2002 (Both 2010). It seems therefore paradoxical that a previous Dutch study did not observe advancements in spring arrival in Dutch flycatchers breeding in the Hoge Veluwe (Both & Visser 2001). One may argue that the fast migration and tight correlation between winter departure and spring arrival were not representative. If the spring of 2014 happened to be highly favourable and lacked adverse conditions en route, this may also explain why pied flycatchers migrated at rates that are among the fastest recorded in smaller migrants (e.g. Tøttrup *et al.* 2012a,b; Kristensen, Tøttrup & Thorup 2013; Lemke *et al.* 2013; McKinnon, Fraser & Stutchbury 2013; Hahn *et al.* 2014; McKinnon *et al.* 2014). However, the few spring tracks of Dutch flycatcher males from previous years (Ouwehand *et al.* 2016) exhibited similar (2013: mean = 14 day, $n = 2$) or a slightly longer migration durations (2012: mean = 19.5 day, $n = 2$) compared to 2014, suggesting that spring migration in flycatchers is generally fast. Additionally, spring arrival in 2014 in our study area was not especially early, again suggesting that conditions were not exceptionally favourable (Both, Bijlsma & Ouwehand 2016).

It is important to note that variation in departure may result from conditions at the wintering grounds, which can vary in time and space (Saino *et al.* 2007; Studds & Marra 2007). In particular, wintering latitude is expected to affect rainfall patterns and hence habitat quality, and unfortunately our data did not allow to investigate whether this associates with departure date. Pied flycatchers occupy a range of wintering habitats in a landscape characterized by gradients in rainfall (Morel & Morel 1992; Salewski, Bairlein & Leisler 2002a; Salewski *et al.* 2002b; Dowsett 2010) that create complex spatiotemporal variation in conditions important for spring fuelling. Annual variation in departure conditions can thus potentially explain variation in breeding ground arrival, which is in agreement with the fluctuations in the strength of repeatability in arrival dates among sets of years in our flycatcher population (Both, Bijlsma & Ouwehand 2016).

Dutch pied flycatchers seem to have limited options to adjust their arrival at the breeding grounds apart from advancing departure date. In contrast, other long-distance migrants with slower and more variable migration rates may advance spring arrival by faster migration. The ability of pied flycatchers to advance arrival dates in response to rapid climate change might be slowed down by years with harsh circumstances in winter, or by years in which selection against early departing birds if they encounter deteriorating conditions during spring fuelling or migration. Interestingly, later migrating flycatchers that head to Northern Europe (e.g. Ahola *et al.* 2004) experience improved temperatures during migration, which were held responsible for advanced arrival dates at their breeding grounds. So, in contrast to the birds in

our study, they possibly may still have the ability to increase their migration speed. Thus, between pied flycatchers' populations, the means by which these long-distance migrants can successfully track environmental changes at their breeding grounds may vary. Individual tracking over multiple years in various populations will help disentangling whether migration timing is indeed always tight in pied flycatchers, with selective mortality or flexible departure decisions driving variation in arrival timing across years.

Authors' contributions

J.O. and C.B. designed and carried out the study, J.O. analysed the data, and J.O. and C.B. wrote the manuscript.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.k6q68> (Ouwehand & Both 2016b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Timing of arrival and egg laying of pied flycatchers in 2013–2014 for control birds and geolocator birds.

Fig. S2. Timing of arrival and reproduction in 2013 of geolocator birds that returned or not.

Fig. S3. Correlations between migratory events over 2013–2014.

Fig. S4. Twilight times, longitude and latitude across 2013–2014 on geolocator birds with LL.

Table S1. Sample sizes and return percentages of birds with and without geolocators.

Table S2. Summary of sex differences in annual cycle events.

Table S3. Raw data of timing and duration of annual cycle events for geolocator birds with LL.

Table S4. Summary of relations among annual cycle events accounted for sex differences.